

Natural tree regeneration along a chronosequence of dieback-affected Norway spruce stands



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Picture: Generated with AI

Schematic: Generated with phylopic (Keesey, 2024)

Abstract

Production forests with Norway spruce monocultures are experiencing mass mortality in Europe, due to climate change and biotic pests. In The Netherlands, Hart van Drenthe, rewilding management is utilized to create a more natural sustainable forest. In this study, I investigated how a rewilding management in spruce forests impacts the forest composition and diversity over time. To achieve this, I conducted field data collection across 22 plots situated within spruce forest sites arranged along a temporal gradient, or chronosequence, reflecting varying stages of dieback progression over 23 years. Analyses included regression models over the years to identify changes in species diversity and PCA to identify changes in species composition. Results indicated along the chronosequence the diversity increases based on species abundance and Shannon diversity index. Approximately 6 years after first dieback Norway spruce stands, the proportion of new species and the total number of individuals increases. Indicated that the composition of species is similar in the first years since first dieback, but started to change around 14 years of being affected and changes again after 23 years of affected. Along the chronosequence (time since first dieback), the diversity increases. This study shows that the species composition along the chronosequence of dieback from monocultural Norway spruce stands, changed from a spruce forest to a more diverse forest. Nevertheless, the direction of the compositional change does not appear to be unidirectional, indicating the context dependency and complexity of these long-term processes.

Summary

Productiebossen met monoculturen van fijnsparren ondervinden massale sterfte in Europa als gevolg van klimaatverandering en biotische plagen. In Nederland wordt in het Hart van Drenthe rewilding management toegepast om een natuurlijker en duurzamer bos te creëren. In deze studie onderzocht ik hoe rewilding management in fijnsparbossen, de bos samenstelling en diversiteit in de loop van de tijd beïnvloedt. Om dit te bereiken, heb ik veldgegevens verzameld op 22 percelen in fijnspar bossen, gerangschikt langs een temporele gradiënt of chronosequentie, die verschillende stadia van achteruitgang gedurende 23 jaar weerspiegelt. De analyses omvatten regressiemodellen over de jaren om veranderingen in soortendiversiteit te identificeren en PCA om veranderingen in soortensamenstelling te identificeren. De resultaten geven aan dat langs de chronosequentie de diversiteit toeneemt op basis van soortenrijkdom en de Shannon-diversiteitsindex. Ongeveer 6 jaar na de eerste achteruitgang van fijnsparren, neemt de hoeveelheid soorten en het totale aantal individuen toe. Het wijst erop dat de samenstelling van soorten in de eerste jaren na de eerste achteruitgang vergelijkbaar is, maar begint te veranderen rond 14 jaar na de eerste achteruitgang en verandert opnieuw na 23 jaar. Langs de chronosequentie (tijd sinds de eerste achteruitgang) neemt de diversiteit toe. Deze studie toont aan dat de soortensamenstelling veranderd langs de chronosequentie van omvallen van monoculturele fijnsparbossen van een sparrenbos naar een meer divers bos. Desalniettemin lijkt de richting van de samenstellingsverandering niet eenduidig te zijn, wat wijst op de contextafhankelijkheid en complexiteit van deze langetermijnprocessen.

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Introduction

Forests in Europe have far-reaching benefits in numerous aspects. Besides the economic importance of timber production, forests offer benefits in for instance climate regulation and water control. The contribution as climate regulations can be found in carbon and nitrogen storage and absorbing carbon dioxide. The contribution in water control is in providing clean water, but also stocking water and lowering evaporation (*Forests and Forestry*, 2023). Different forest management types focus on diverse aspects of the forest, understanding all the effects on forests of different forest management types is important to create a more sustainable forest (Simler-Williamson et al., 2019). In timber producing forests, the management has to balance the economic benefits versus the ecological benefits. A timber producing tree which was introduced in many parts of Europe in the 19th century, is the Norway spruce (*Picea abies*) (Klimo & European Forest Institute, 2000). Norway spruce can grow on low soil fertility and a range of climate conditions, while being more productive for forestry purposes than more common native species. Norway spruce wood is a high demanded construction wood as, it is light in weight, and it is also a preferred wood for bioenergy (Jandl, 2020). Norway spruce is a fast grower and prefers average acidic (5.0-6.5 pH) and well-drained sandy soils (Ekö et al., 2008; Oulehle & Hruška, 2005). Typically, Norway spruce forests are planted as monocultural forest. While such single-species forests are economically beneficial, they can be disruptive for the sustainability of the forest, as they are more susceptible for abiotic stressors (e.g., climate change) and biotic stressors (e.g., pests). Ongoing climate change has a large influence on Norway spruce, as the increased periods of rain in the autumn and winter combined with long periods of extreme drought in spring and summer are increasing the stress and mortality survivability of the trees. In addition, due to the effects of climate change, Norway spruce seems also more vulnerable to outbreaks of the European spruce bark beetle (*Ips typographus*), a native bark beetle that is a pest species to Norway spruce, and can affect complete forests. Indeed, outbreaks of bark beetles are often correlated to periods of extreme drought or wet periods, happening due to the stress of Norway spruce because of the extreme climate (Obladen et al., 2021). When in large numbers, bark beetles can even affect healthy trees. Norway spruce infected by *I. typographus* goes through 4 stages: alive trees have green

needles (1), when first infected the trees look like stage 1 but with brown needles (2), after being infected for a while, the trees have lost part of their needles and have holes in the bark (3). and lastly the trees are still standing up but have hardly any bark left (4) (Storaunet, 2004; Wermelinger, 2004). The Norway spruce is an evergreen tree species, increasing the contrast between affected and non-affected trees. Management in Norway spruce production forests aims to minimize the attack of the bark beetles on living trees. Historically each infected tree was logged and debarked, which was labor intensive and therefore this management ceased to exist. A common used method is clearing windthrows, afterwards the already infected trees can be removed (Havašová et al., 2017). After massive diebacks of Norway spruce, different management strategies are in place, like replacing Norway spruce with new Norway spruce trees, by actively replacing Norway spruce with different tree species by reforestation/replantation or by rewilding management, such as hands-of management. Production forests lack biodiversity, due to single-species tree stands, have a negative impact on the worldwide biodiversity crisis. By increasing the biodiversity in monocultural forests, a more sustainable and future-proof forest is created. (Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019).

Rewilding management type abandons the production forest target, and aims to create a more natural sustainable forest. The, by stressors, affected Norway spruce are not removed, and will turn into dead standing trees (snags) or lying dead wood. Norway spruce increase the acidity of the soil, creating a suitable environment for the species to grow (Uroz et al., 2016). Therefore is a risk of recreating a monocultural Norway spruce forest, despite efforts to create a more natural diverse forest (Zeppenfeld et al., 2015). This type of management increases structural heterogeneity over a long period of time and higher chance of increased biodiversity in temperate forests (Thers et al., 2019). Different management types after massive diebacks of Norway spruce, showed minimal influence on the number of spruce bark beetles, however natural disturbances like storms, fire and drought had a large effect on the increase in number of spruce bark beetle (Fora & Balog, 2021; Schlyter et al., 2006)

In the Netherlands, Norway spruce was added as production trees from the mid-nineteenth century onwards. The sandy soils (in the East and South of the country) combined with a maritime climate created favorable growing conditions for the trees. However, ongoing long-term shifts in temperature and weather patterns are currently causing less favorable

conditions for Norway spruce trees, increasing the abiotic stress of the trees and, making the trees more susceptible for biotic pests (*I. typographus*). Management has adopted new strategies to handle the effects of *I. typographus*, abstaining from preventing the infection of the pest or logging the affected trees, but a more natural management type often being rewilding.

In this study, it is aimed to assess the impacts of a rewilding management in spruce forests on the forest composition and diversity over time. For this, I studied woody vegetation recruitment in Norway spruce forest sites in Drenthe, The Netherlands, along a chronosequence of time since (indications) of spruce dieback. In 22 plots of 10m x 10m along this chronosequence, I recorded tree species diversity and evenness. Using this space for time substitution, I assessed changes in type of woody vegetation composition and nativeness over time, with a focus on the changes in survival of Norway spruce in different size classes.

Materials and methods

Study area

The study area (Hart van Drenthe) is located in the north of The Netherlands, in the center of the province Drenthe (52°54'N 6°36'E) and is part of the National Park Drentsche Aa (figure 1A) and is managed by Staatsbosbeheer. A small part is a Natura-2000 area (The Elperstroom). Hart van Drenthe contains approximately 5000ha and is a collaboration of 3 forest units since 1980 (Old Grol, 2024). The mean elevation is approximately 20m NAP, with a mean annual temperature of 11.28 °C and an annual rainfall of 822,825mm (weather station: Hoogeveen, average of 2013-2023).

The study area has a moderate maritime climate, formed in a stream valley with nutrient-poor sandy soil, with a shallow clayish top horizon. Historically, the swampy area was wild and inaccessible to humans, but human interventions changed the landscape over time by mining the peat after which, the area became an open sandy area with massive sand drifts. Heath flourished on the open sandy area, combined with intensive livestock grazing. Afterwards the area planting with trees for forestry purposes (Norway spruce, Scots pine and others), creating the forests that still exists. The forest was partially planted by Staatsbosbeheer and has been managed by them ever since.

Therefore, the vegetation is dominated mainly by species planted in the area, such as dominant woody vegetation like Norway spruce (*Picea abies*), Red oak (*Quercus rubra*), Japanese larch (*Larix Kaempferi*) and common beech (*Fagus sylvatica*). Dominant vegetation in the area without human intervention such as the European heath (*Calluna vulgaris*) and on nutrient poor wet soils and bogs is common cottongrass (*Eriophorum angustifolium*). The natural habitats supporting diverse wildlife populations, among which populations of roe deer, wolves, beavers, and numerous species of woodpeckers, underscoring its ecological significance.

The study area attracts a diverse range of visitors throughout the year, including hikers and cyclists, but there are no cars allowed in the area. The area has a network of asphalted thoroughfares, stone pathways, and natural unpaved trails.

Site selection

Sites in the area are outlined by ditches and contain a site number, the area is merged out of 3 forestries Hooghalen (red), Grolloo (blue) and Schoonloo (figure 1B). Schoonloo is removed from this study, due to year-round grazing by cattle. In general, sites were selected with monocultures of Norway spruce and with a known time since first dieback was noticed in the stands by Staatsbosbeheer. Also, sites required sizes larger than 10.000m². In each site with a known time since first noticed dieback, three plots of 10m x 10m were placed in sites with corresponding years since first affected. In unaffected sites (i.e. with no observed die back of individual Norway spruce at time of study) four plots were selected; either in the same site or in different sites. In order to create a chronosequence, a wide variety of different sites with different years since first affected are needed. Therefore, data from Hooghalen and Grolloo are pooled together. In Hooghalen sites appear to be affected earlier compared to Grolloo. In total I sampled 22 plots along a chronosequence of 23 years (table 1), with 4 sites in forestry Hooghalen and 8 sites in forestry Grolloo.

Table 1: sampled sites in study area

Year first affected	Sites sampled	Plots sampled	Location
2000	2	3	Hooghalen
2003	2	3	Hooghalen + Grolloo
2009	1	3	Hooghalen
2017	1	3	Grolloo
2018	3	3	Grolloo
2020	1	3	Grolloo
unaffected	3	4	Hooghalen + Grolloo

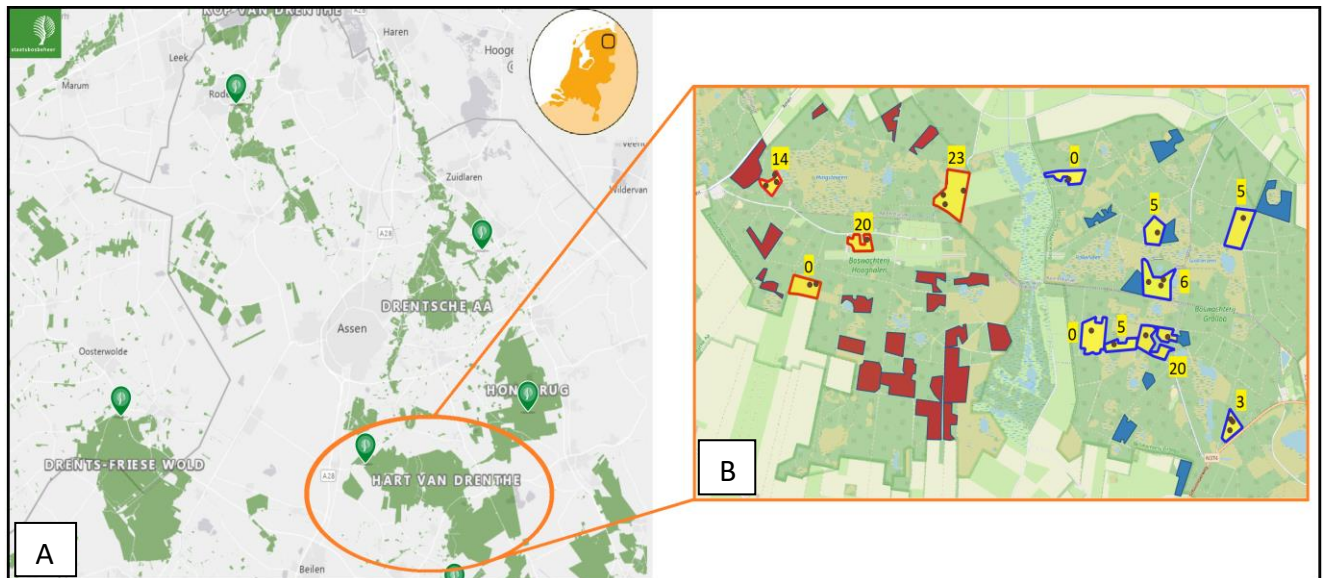


Figure 1: Location of Hart van Drenthe in The Netherlands with the study area

Showing the location of the study site, A) Hart van Drenthe in The Netherlands and the province of Drenthe. B) the sites with Norway spruce stands in Hart van Drenthe with in red the Hooghalen area and in blue the Grolloo area. In yellow the studied sites, brown dots showing the number of plots in the site and the number in yellow block corresponding to the number of years since first being affected.

Fieldwork was performed during summer (June – August) of 2023, with an average temperature of 17,7 Celsius (*Weergegevens Hoogeveen 2023 - Weerstatistieken KNMI, n.d.*) and an average rainfall of 94,3mm (*Jaar 2023, n.d.*).

Sampling design and data collection

Measured variables at plot level (10m x 10m)

Percentage cover of grass, moss and bare soil was estimated in percentages at plot level. Dead wood on the ground was divided into 3 classes based on diameter size (<5cm, 5-10cm and >10cm) and visually estimated in percentages covering the ground. The humus layer thickness (cm) was measured as the horizon layer (leaf litter + decomposition layer + humus layer) in the center of the plot, but at least 1m away from a tree (trunk).

The total number of trees in the plot was counted, with each tree divided into 4 'vitality' classes: standing alive, standing dead, lying down alive and lying down dead. The average tree

density is the tree density divided by the total number of trees. In addition, I counted the number of tree stumps in the plot as indicator of human interference (logging). The woody vegetation height from 40cm high onwards, was measured at individual level; below 40cm an estimation of the percentage cover.

For the canopy cover a photo was made in the center of the plot at least 1m away from a standing tree at 1.5m height. Canopy openness was calculated with ImageJ (Schneider et al., 2012). For that, I configured the picture to black and white, limiting the threshold to show everything of the tree as white, such as leaves and branches, and the rest as black. Canopy openness was described as the fraction of black pixels compared to the whole image.

To have a broader indication of the forest composition of the site, I selected 10 nearest mature trees outside the plot and recorded species identify and whether they were alive or dead.

Measured variables at subplot level (1m x 1m)

Each 1m x 1m plot was subdivided in hundred subplots of 1m², and in each subplot the individual woody species (> 40 cm tall) were scored. First, I noted the species and the number of stems at the bottom. The length of the longest tribe was measured as maximal length (length of individual if had grown straight up), and as normal length (length of individual). The diameter was measured or calculated based on the circumference in cm. The diameter was measured as closely to the soil as possible, while the circumference of trees was measured at DBH (diameter at breast height). Further, it was identified whether the individual had signs of browsing (twigs of branches bitten of). Finally, the individual was scored as being alive (0) or dead (1). Decomposition of dead Norway spruce was scored on the level of decomposition, with alive individuals scoring a (0) and dead individuals ranging from low to high (1-4) as described by (Smith et al., 2009).

Data analyses

All analyses were performed using R Statistical Software version 4.2.1 (R Core Team, 2021). Data were reformed and visualized with the use of tidyverse and tidyr, and the analyses were performed with lme4 and lmerTest

Differences in diversity

Diversity was referred to as the different measures of species richness, including species diversity and evenness. In this study, multiple values to indicate diversity were measured. Species abundance was calculated as the total number of species recorded in each site. Shannon diversity index (H') was calculated with R vegan package (Oksanen et al., 2022) based on the formula:

$$H' = - \sum_{i=1}^S p_i \log_b p_i$$

where p_i represents the number of individuals of species in a plot divided by the total number of individuals in the plot, \log is the normal logarithm, and \sum is the sum of the calculations. The Shannon diversity index incorporates the species richness and proportion of each species in sampled plots.

Evenness in species abundance was studied with Buzas Gibson's evenness index (E), calculated with the formula:

$$E = \frac{e^{H'}}{S}$$

where H' is the Shannon diversity index, e is the natural logarithm base, and S is the total number of species. Evenness visualizes the equitability of abundances of different species, varying from 0 indicating different abundance in the species to 1 indicating all species have the same abundance.

The dominance of Norway spruce was calculated by dividing Norway spruce individuals in a plot (N_x) by the total number of individuals in the plot (N_{tot}).

$$D = \frac{N_x}{N_{tot}}$$

I tested if the time / year since first noticed dieback affected the various diversity indices (species richness, Shannon diversity, Buzas-Gibson Evenness, Norway spruce dominance) using lm/glm models. When the assumptions of normality and homogeneity were not

reached, transformations were performed. Therefore, in species richness a poisson distribution was used, in the Shannon diversity the data was square root transformed finally in the Norway spruce dominance the data was exponentiated. The type and origin data were transformed with a binomial distribution. In the graphs untransformed data are shown. The gaussian distributed models were tested with a t-test ($p < 0,05$) and the explained variance of adjusted R^2 . The poisson and gamma distributed models were tested with a Goodness-of-fit-test ($\chi^2 < 0,05$). The best model was chosen based on lowest AIC-value and ecological relevance.

Types of woody vegetation

Woody species were grouped into deciduous or coniferous type and native or non-native origin (S1). In order to identify the changes occurring in species diversity over the years, the changes in types and origin of woody vegetation were identified. Changes over time between type and origin was tested with a generalized linear model (family = binomial).

Changes in species composition: multivariate analyses

Sites and species abundance was studied with a principal component analysis (PCA) biplot. A biplot analysis is a multivariate graphical representation, showing the distribution of species compared to all species. The PCA analyses were performed with multiple R packages, like ggfortify, ggalt, corrr, ggcorrplot, FactoMineR and factoextra. Patterns in species composition of woody vegetation along the chronosequence were also explored with a PCA, based on the abundance in grouped years (plots of same year of first recorded dieback).

Results

1. Changes in species diversity

The species richness, expressed in total identified woody species per plot, increased along the chronosequence since first noted dieback (figure 2A). In unaffected sites (year = 0), low species richness was found with an average of 1.5 (table 6). The average species richness increased over time (table 6), with the highest species richness (7.67) found in the sites with the longest history of dieback (23 years since first dieback; table 6). The best fitted model for species richness according to the AIC-value (81.58) includes Years (since first noted dieback) and number of tree stumps (table 2). Indicating the longer an area has had since first dieback and a lower tree stumps number in the area, a higher number of species can be found.

Table 2: Results of GLM (repeated measures ANOVA design) with poisson distribution, showing significance (P-value) changes along the chronosequence. The best fitted model is as well shown, included with the AIC and the Chi² value

Effect: Species richness	Estimate	P-value	AIC	Chi ²
Years	0.06733	6.32e-07	88.08	3.347e-07
Years + tree stumps	0.02865 + - 0.25423		81.58	3.347e-07 + 0.003557

The Shannon diversity index (H') is lowest at unaffected sites ($H'=0.0036$; mean=0.13) (table1). It increases along the chronosequence, but is highest around 14 years after first noted dieback (figure 2C) and stabilizes afterwards ($H'=1.163$; mean=0.81). The best fitted model for Shannon diversity according to the AIC-value (-0.688) only includes Years (table 3).

Table 3: Results of LM (repeated measures ANOVA design) with a square root transformation, showing significance (P-value) changes along the chronosequence. The best fitted model is as well shown, included with the AIC and the F-value. R^2 of best fitted model = 0.7236

Effect: Shannon diversity	Estimate	P-value	AIC	F-value
Years	0.028284	0.0002	-0.688	0.0001997

Buzas Gibson evenness (E) differs over years and has a downward trend (figure 2D). The highest Buzas Gibson evenness values were noted at 0 years and 14 years after first noted spruce dieback (table 6). The best fitted model according AIC-value (-0.553) for Buzas Gibson evenness includes Years, percentage of mosses, humus layer (cm), percentage of woody vegetation <40cm and number of tree stumps (table 4).

Table 4: Results of LM (repeated measures ANOVA design) with a poisson distribution, showing significance (P-value) changes along the chronosequence. The best fitted model is as well shown, included with the AIC and the F-value. R^2 of best fitted model = -0.04421

Effect: Buzas Gibson evenness	Estimate	P-value	AIC	F-value
Years	-0.010151	0.0587	-7.414	0.058
Years + Mosses + Humus layer + Woody Vegetation <30cm + tree stumps	-0.0086 + 0.00023 + -0.0176 + -0.0020 + 0.02008	0.537	-0.553	0.086 + 0.985 + 0.613 + 0.606 + 0.637

The best fitted model (AIC-value: 11.54) for dominance of *P. abies* includes Years and the fraction of dead trees in the area (table 5). Dominance of *P. abies* differs over the years and shows a downward trend (table 6). The lowest *P. abies* dominance was at 14 years after first noted dieback, while the latest years (20 and 23 years) have similar values as the earlier years (3 and 5 years) (figure 2E).

Table 5: Results of LM (repeated measures ANOVA design) with a square transformation, showing significance (P-value) changes along the chronosequence. For the Surrounding Trees dead fraction, the same model was used, but without the square transformation. The best fitted model is as well shown, included with the AIC and the F-value. R^2 of best fitted model = 0.7236

Effect: Dominance <i>P. abies</i>	Estimate	P-value	AIC	F-value
Years	-0.013351	0.168	15.48543	0.1682
Years + Surrounding Trees dead (fraction)	0.002515 + - 0.447300	0.1798	11.5462	0.2267 + 0.1530

Table 6: Means of all variables per year

Affected Years	Mean total species	Mean Shannon diversity	Mean Buzas Gibson evenness	Mean Dominance P. abies	Mean Total
0	1,50	0,13	0,67	0,965	38,50
3	2,00	0,03	0,39	0,6	8,00
5	1,67	0,08	0,22	0,633	10,00
6	3,00	0,11	0,40	0,851	63,33
14	4,67	0,81	0,50	0,381	119,67
20	5,67	0,47	0,29	0,678	247,33
23	7,67	0,81	0,30	0,676	213,67

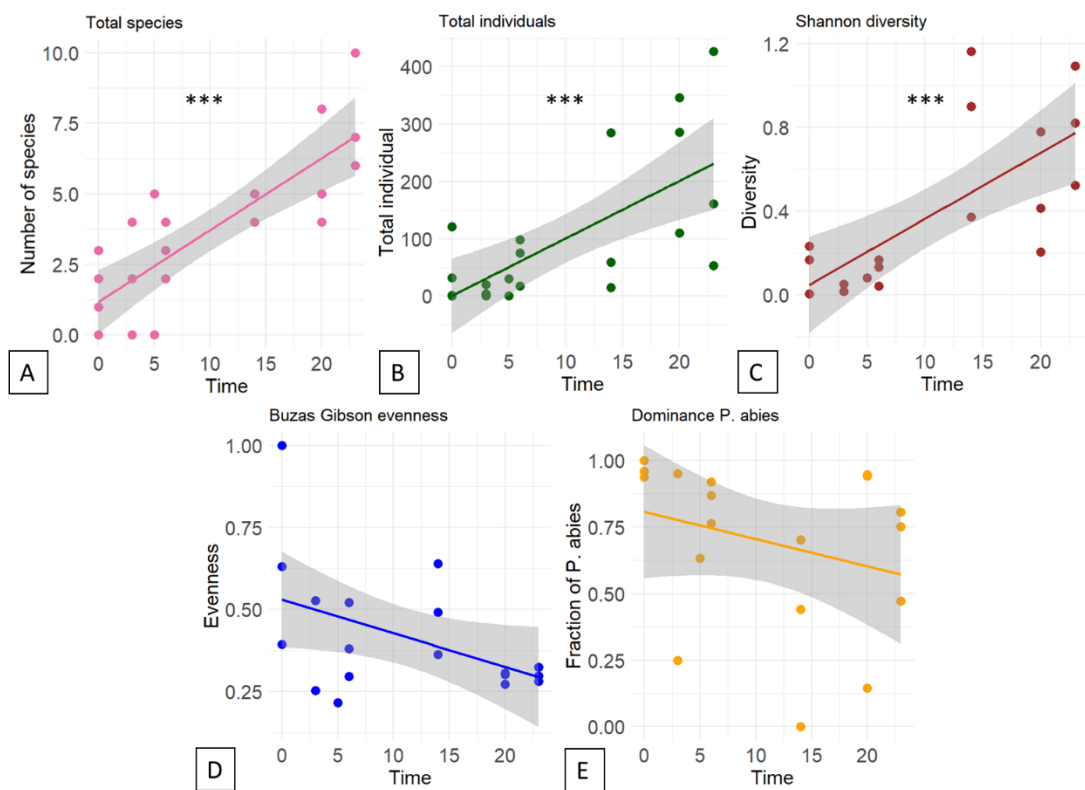


Figure 2: Linear changes of the different species diversity indices and values

The different panels in this graph show different species diversity indices and values. Each of the panes has on the x-axis the time since first dieback noted, and all panels have a linear regression line. A. the total number of species in each plot is visualized. B. the total number of individuals in each plot is visualized. C. the Shannon diversity index is visualized. D. The Buzas Gibson evenness index is visualized, with 1 is complete even distribution and 0 is completely uneven distribution. E. the dominance of P. abies, based on the number of P. abies individuals compared to total number of individuals is visualized.

2. Changes in type and origin of woody vegetation (coniferous vs. deciduous, native vs. non-native)

2.1 Coniferous or deciduous woody vegetation

Along the chronosequence, the percentage of coniferous trees goes down and the percentage of deciduous trees goes up (figure 3). The decrease in coniferous trees is highly related to the years since first recorded dieback ($p = 2.59e-11$). Overall, it shows that time since first dieback has a significant effect on the percentage coniferous versus deciduous trees, combined with the decrease of coniferous trees over time by 0.0664 (table 7). This trend is also visible when looking at the total number of deciduous and coniferous trees over time (table 8).

Table 7: Results of GLM (repeated measures ANOVA design) with family=binomial, showing significance (P-value) changes along the chronosequence. Best fitted model is as well shown, included with the AIC.

Predictor	Estimate	Standard error	Z-value	Pr (> z)
Type ~ Years	-0.0664	0.0099	-6.668	2.59e-11 ***

Table 8: The change of type along the chronosequence

Type	0 years	3 years	5 years	6 years	14 years	20 years	23 years
Deciduous	0	2	4	3	107	111	123
Coniferous	178	54	48	194	270	641	528
Total	178	56	52	197	377	752	651

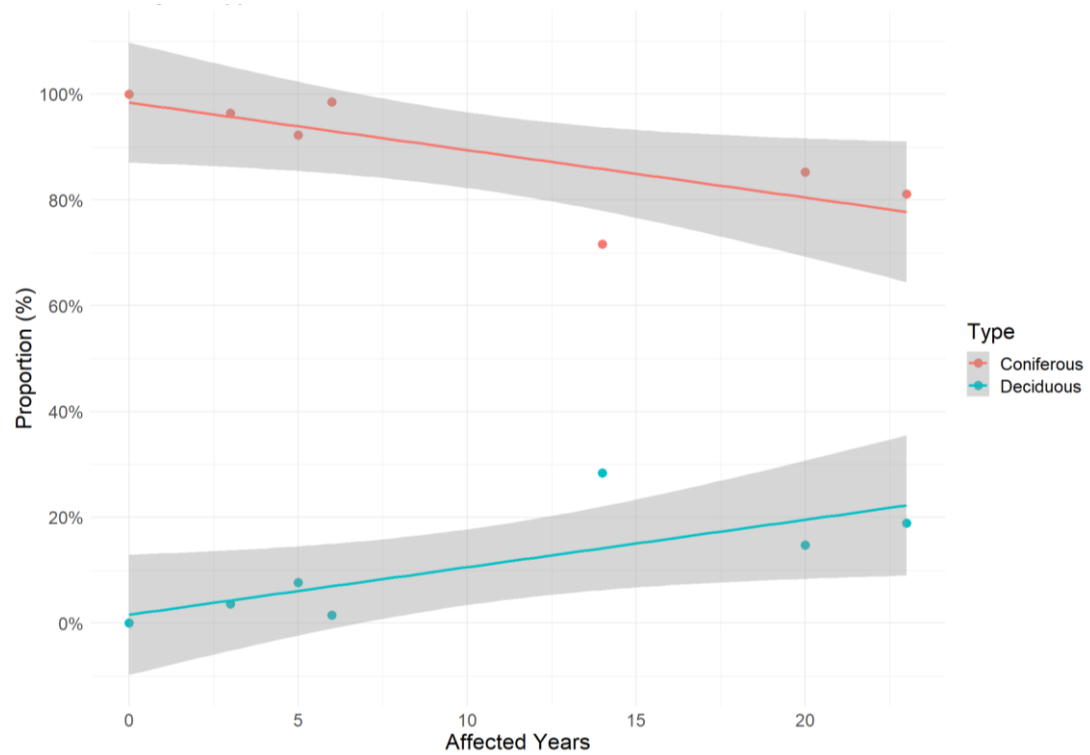


Figure 3: Type change along the chronosequence

The figure shows on the x-axis years since first dieback noted and, on the y-axis, the total trees divided into 2 groups, either coniferous or deciduous. Showing in unaffected sites only coniferous trees are present, at 14 years the percentage of coniferous trees is lowest. Overall, along the chronosequence the percentage of coniferous trees decreases and deciduous trees increases. The proportion is only depended of 2 variables, therefore sum up to 100, the percentage 1 goes up, the other goes down.

2.2 Native or exotic woody vegetation

Along the chronosequence, the ratio of exotic trees goes down, hence the ratio of native trees goes up (figure 4). The decrease in exotic trees is highly related to the years since first affected ($p = 1.34e-10$). Overall, it shows that time since first dieback has a significant effect on the ratio native versus exotic trees, combined with the decrease of exotic trees along the chronosequence by 0.065 (table 9). For both origins, the total number of trees also increases along the chronosequence (table 10).

Table 9: Results of GLM (repeated measures ANOVA design) with family=binomial, showing significance (P-value) changes over time. Best fitted model is as well shown, included with the AIC.

Predictor	Estimate	Standard error	Z-value	Pr (> z)
Type ~ Years	-0.06523	0.01016	-6.423	1.34e-10 ***

Table 10: The change of native trees over the years

Type	0 years	3 years	5 years	6 years	14 years	20 years	23 years
Native	0	2	4	3	100	109	114
Exotic	178	54	48	194	277	643	537
Total	178	56	52	197	377	752	651

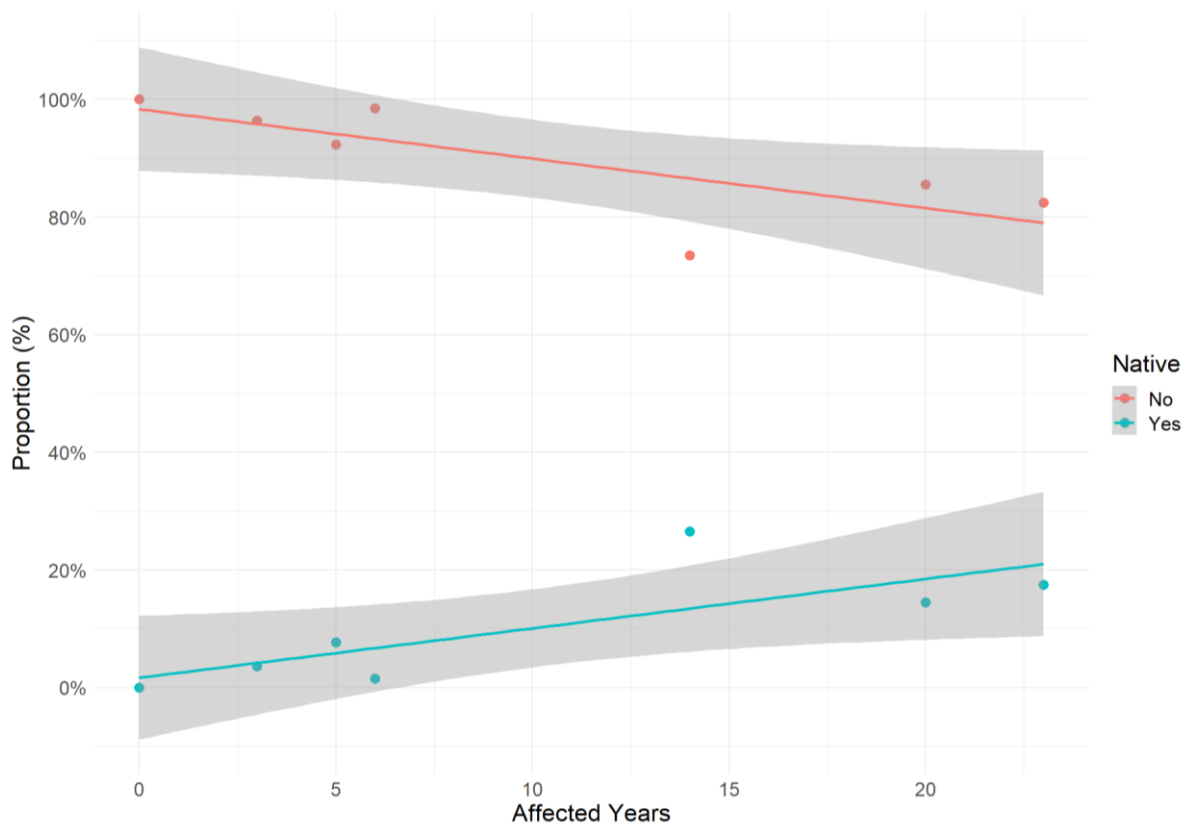


Figure 4: Origin changes along the chronosequence

The figure shows on the x-axis years since first affected and on the y-axis the total trees divided into 2 groups, either native (yes) or exotic (no). Showing in unaffected sites only exotic trees are present, at 14 years after first dieback the percentage of exotic trees is lowest. Overall, along the chronosequence the percentage of exotic trees decreases and native trees increases. The proportion is only depended of 2 variables, therefore sum up to 100, the percentage 1 goes up, the other goes down.

3. Changes in size in Norway spruce regeneration

Along the chronosequence, there is a constant higher number of small-sized Norway spruce recruits, while larger Norway spruce individuals (e.g. > 100 cm) are rare (figure 5). Yet, this number of larger Norway spruce recruits is higher in the older sites since first dieback (from 6 years onwards). Years since first dieback, has no significant effect on the size of regenerated Norway spruce. Plenty environmental variables have a significant effect on the size (table 11).

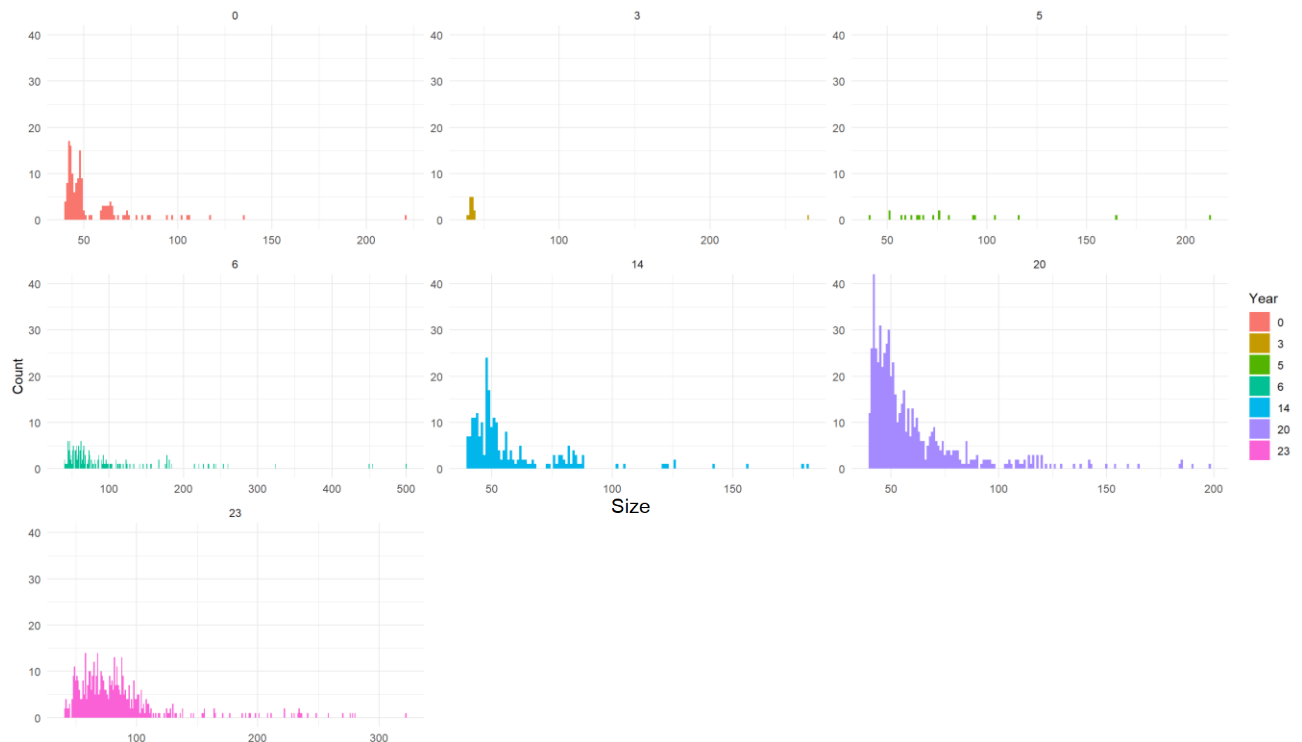


Figure 5: Size changes along the chronosequence in Norway spruces

Each different graph shows a different year since first noted spruce dieback, combined with the color changes. The height of the bar shows the number of individuals with that size. The y-axis is equal in all graphs, the x-axis is not the same in all the graphs.

Table 11: Results of LM (repeated measures ANOVA design, showing significance (P-value) changes over time. Best fitted model is as well shown, included with the AIC.

Effect: size Norway spruce	Estimate	P-value	AIC	Adjusted R ²
Years	0.33	0.0109	17209	0.00326
Total trees + mosses + grasses + dead wood <5cm + woody vegetation <40cm + density + canopy cover + tree logged	-1.80 + 1.34 + 0.86 + 0.95 + -1.58 + -36.92 + -38.82 + -8.65	2.2e-16	16910	0.1689

4. Changes in species composition

To determine changes in species composition along the chronosequence, I performed multiple ordination strategies. Some species are more often found together compared to others (Fig. 6). For example, Birch (Bspe), English oak (Qrob) and Norway spruce (Pabi) point in the same direction with similar arrow lengths, therefore are more commonly found together (figure 6)

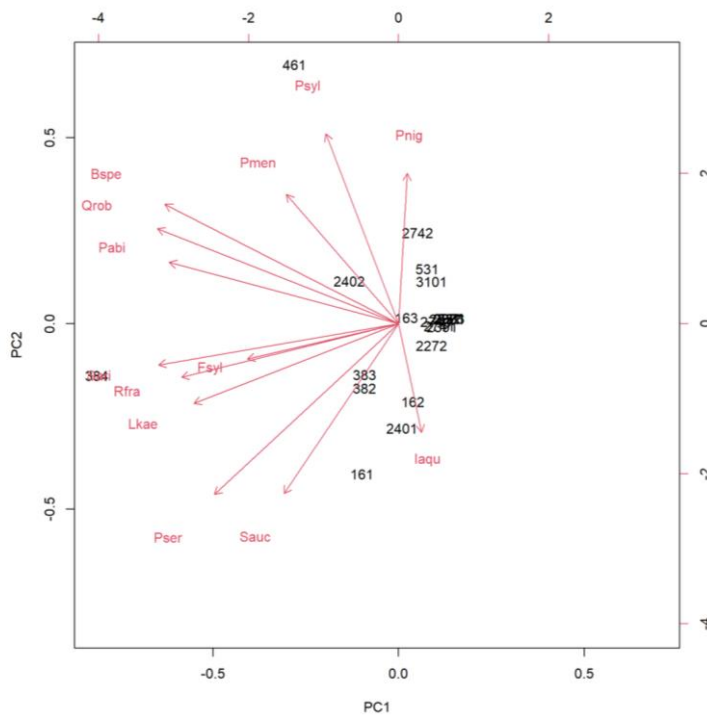


Figure 6: PCA of the species composition

The PCA shows the species based on abundance per plot, the species arrows with similar size and direction are more often found together. The species in the PCA are laqu (*Ilex aquifolium*), Sauc (*Sorbus aucuparia*), Pser (*Prunus serotina*), Lkae (*Larix kaempferi*), Rfra (*Rhamnus frangula*), Fsyl (*Fagus sylvatica*), Sari (*Sorbus aria*), Pabi (*Picea abies*), Qrob (*Quercus robur*), Bspe (*Betula* species), Pmen (*Pseudotsuga menziesii*), Psyl (*Pinus sylvestris*) and Pnig (*Pinus nigra*)

Along the chronosequence, the species composition shows differences with a PCA (figure 7). The PCA indicates that the species composition is similar at overlapping time points of the chronosequence, while it is different when years don't overlap. The x-axis explains 38.86% of the variation and the y-axis explains 17.87%. Each year of first noted spruce dieback was tested 3 times at different locations, each plot is a different point in the graph. The whole triangle shows the range within the species composition lies. The early years (year = 0, 3, 5 and 6)

overlap, while years 14 and 20 overlap with each other but with no other year and 23 years is completely separate from the others.

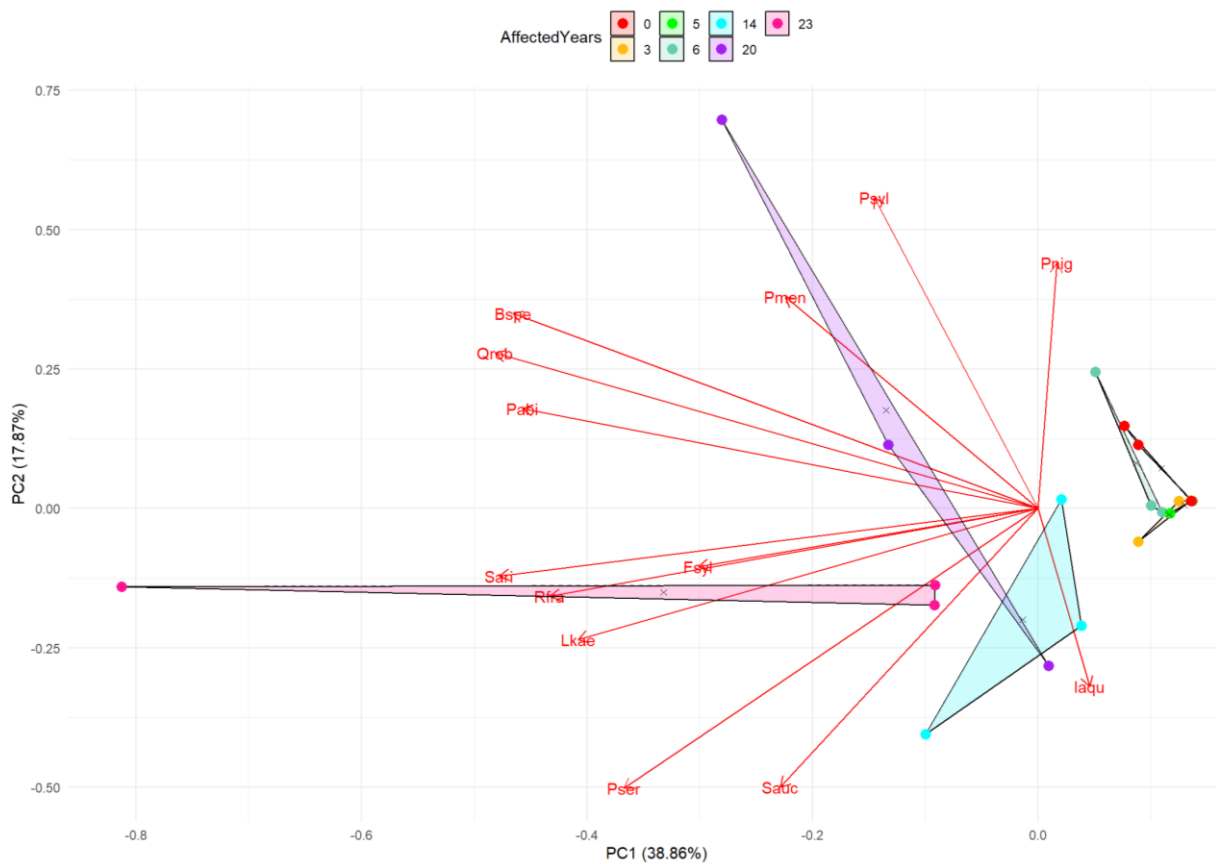


Figure 7: PCA of the species composition changes along the chronosequence

PCA showing the different years since first dieback in different colors, each dot shows a different plot. The arrows are formed similar as in figure 6, based on abundance in a plot. On the right side the early years are grouped together. In the center the middle years (14 and 20 years) are overlapping each other and on the left side the eldest years (23 years) is located not overlapping with any of the other years.

Discussion

In this study the woody vegetation species diversity and composition was assessed along chronosequence of 23 years of Norway spruce dieback. It was shown that the diversity changes along the chronosequence, based on species abundance, the Shannon index and Buzas-Gibson evenness index. The percentage of Norway spruce showed a downward trend. Overall had time along the chronosequence a large and significant effect on the diversity. Also, the woody species composition changed along the chronosequence and tends to become more deciduous and less coniferous, while the percentage of native trees increases. There is no significant effect of years since first dieback on the size of Norway spruce, other factors had a small but significant influence on the size of Norway spruce. The species composition is similar at the unaffected and early affected years, but different compared to later affected years.

4.1 differences in species diversity

Species diversity is a common used representation of ecological change and can be measured in multiple ways, such as species richness and diversity indices (Hamilton, 2005). It was observed that the species richness increases with sites being affected longer. However, years since first affected may not necessarily be the only important determinant in explaining the increase in species richness. Other factors like land use history and location, could have a large influence on the species richness. Due to the sandy soil in Hart van Drenthe, species richness is limited. Species richness reaching an equilibrium is debated (Storch & Okie, 2019), but an equilibrium appears to not have been reached here. Nevertheless there is a limit to the number of species able to grow on sandy soil (Gxasheka et al., 2023). An increase in species richness in earlier years after first affected, as found in this study, was sporadically found previously (Smit & Olff, 1998), however more often species richness increases after at least 10 years (Bard, 1952; Bazzaz, 1975; Monk, 1983). Light availability has a large effect on species richness (Dormann et al., 2020), in this study canopy cover was added as factor but has no significant influence on the species richness. Tree logging in forests is shown to have a significant negative effect on woody vegetation species richness (Clark & Covey, 2012), as also shown in this study. Shannon diversity increases in this study, with a positive peak in Shannon diversity after 14 years of first affected. Shannon diversity increases in the absence of grazing and decreases with grazing, often no significant changes were found under grazing (Lyseng et

al., 2018; Ramirez et al., 2019). In this study the effects of grazing were not studied, however grazing was only observed in deciduous woody vegetation and not in coniferous woody vegetation, while at the same time the number of deciduous trees and species increases along the chronosequence. The evenness studied with Buzas Gibson showed a decrease in evenness overtime, however the trend was not significant. The evenness showed 2 positive peaks at the start (0 and 3 years) and again in the middle (6 and 14 years). Changes in evenness were best explained by multiple variables, year since first affected, the percentage of ground covered by moss, the thickness of the humus layer, the percentage of woody vegetation smaller than 30cm and number tree stumps. Evenness shows more often no change in temperate forests, however long after thinning a small decrease in evenness has been found (Palm et al., 2022; Xie et al., 2023). The dominance in Norway spruce seemed constant along the chronosequence, with overall a higher number of low Norway spruce dominant sites in areas with earlier first dieback. A Norway spruce dominant forest remains a Norway spruce forest, despite mass mortality (Ekö et al., 2008; Fora & Balog, 2021; Hentschel et al., 2014; Huth et al., 2017; A. Kupferschmid et al., 2002; A. D. Kupferschmid et al., 2006; Pretzsch et al., 2020). However, in this study an increase in species richness was found.

4.2 differences in type and origin

A decrease in coniferous trees and tree species combined with a decrease in exotic tree species was shown in this study. Overall research has shown that rewilding causes a decrease in monocultural trees. Natural regeneration of different species in a monocultural forest is mostly due to seeds infiltrating from outside the forest (Dey et al., 2019). Mixed forests increase diversity in other groups as well, such as invertebrates and birds, however this was not studied here. (Leidinger et al., 2021; Riffell et al., 2011; Zaitsev et al., 2014). The proportion of type and origin changed along the chronosequence. Nevertheless, the absolute numbers showed a decrease in regeneration at timepoint 3 and 5. This decrease in absolute numbers is hard to explain, but most of its variation is likely to be described to a change in location (Hooghalen/Grolloo) or to a change in location of the plot within the site. Lastly the results shown are of a chronosequence, and therefore do not show actual change overtime.

4.3 Changes in size in Norway spruce regeneration

Norway spruce is a fast-growing tree species, and the growth rate is density depended, although thinning doesn't have an effect on the growth rate. While increase thinning,

increases volume growth. (Gizachew & Brunner, 2011). In agreement to this study, here it was shown that a lot of variables affect the size of Norway spruce despite thinning (tree logs) and years, but the effects of volume growth were not studied here. Long periods of drought favors small Norway spruce (Pretzsch et al., 2018). With climate change and longer periods of drought, a preference for small trees can be explained. In this study the whole study area has a similar climate including similar drought periods. Individual Norway spruce trees experience different growth rates, mostly due to fitness differences (Avanzi et al., 2020). In this study hardly any regenerated large adult trees were found, only a few individual trees gain the opportunity to grow into a large adult tree, but without optimal climate condition this is not reached.

4.4 Species composition changes

Overtime the monocultural forest changed into a more diverse forest. The species composition changed along the chronosequence. Previous studies shown monocultural Norway spruce forests remain, even after less human influence in forests (Ekö et al., 2008; Fora & Balog, 2021; Hentschel et al., 2014; Huth et al., 2017; A. Kupferschmid et al., 2002; A. D. Kupferschmid et al., 2006; Pretzsch et al., 2020). Although other studies shown a decrease in monocultural Norway spruce forests, however it is very time consuming (Térauds et al., 2011). In this study it was shown that the change in species composition occurs around 14 years after first affected. There is large time gap between first affected 6 years ago and 14 years ago. The species composition change has a direction, however the direction itself is hard to predict. Even though there is still a large percentage of Norway spruce in sites affected first at least 14 years ago, the species composition is completely different compared to the species composition at earlier or unaffected sites with mostly Norway spruce.

4.5 Future research

The Hart van Drenthe study area, used to be characterized by patches of monocultural Norway spruce forest, with trees of the same age and a limit number of regeneration of any species. By decreasing human influence with a rewilding management in the forest, there is a trend towards a more diverse forest. Nevertheless, this study showed a small time period with quite some significant holes in the chronosequence. Repeating the study with the same sites in approximately 5 years, the sites have evolved into a time period similar to this study. Showing

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a more accurate representation of the actual changes over time, including the effect of sites on a small scale within Hart van Drenthe.

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References

- Avanzi, C., Heer, K., Büntgen, U., Labriola, M., Leonardi, S., Opgenoorth, L., Piermattei, A., Urbinati, C., Vendramin, G. G., & Piotti, A. (2020). Individual reproductive success in Norway spruce natural populations depends on growth rate, age and sensitivity to temperature. *Heredity*, *124*(6), 685–698. <https://doi.org/10.1038/s41437-020-0305-0>
- Bard, G. E. (1952). Secondary Succession on the Piedmont of New Jersey. *Ecological Monographs*, *22*(3), 195–215. <https://doi.org/10.2307/1943565>
- Bazzaz, F. A. (1975). Plant Species Diversity in Old-Field Successional Ecosystems in Southern Illinois. *Ecology*, *56*(2), 485–488. <https://doi.org/10.2307/1934981>
- Clark, J. A., & Covey, K. R. (2012). Tree species richness and the logging of natural forests: A meta-analysis. *Forest Ecology and Management*, *276*, 146–153. <https://doi.org/10.1016/j.foreco.2012.04.001>
- Dey, D. C., Knapp, B. O., Battaglia, M. A., Deal, R. L., Hart, J. L., O'Hara, K. L., Schweitzer, C. J., & Schuler, T. M. (2019). Barriers to natural regeneration in temperate forests across the USA. *New Forests*, *50*(1), 11–40. <https://doi.org/10.1007/s11056-018-09694-6>
- Dormann, C. F., Bagnara, M., Boch, S., Hinderling, J., Janeiro-Otero, A., Schäfer, D., Schall, P., & Hartig, F. (2020). Plant species richness increases with light availability, but not variability, in temperate forests understorey. *BMC Ecology*, *20*(1), 43. <https://doi.org/10.1186/s12898-020-00311-9>
- Ekö, P.-M., Johansson, U., Petersson, N., Bergqvist, J., Elfving, B., & Frisk, J. (2008). Current growth differences of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula pendula* and *Betula pubescens*) in different regions in Sweden.

Scandinavian Journal of Forest Research, 23(4), 307–318.

<https://doi.org/10.1080/02827580802249126>

Fora, C. G., & Balog, A. (2021). The Effects of the Management Strategies on Spruce Bark

Beetles Populations (*Ips typographus* and *Pityogenes chalcographus*), in Apuseni

Natural Park, Romania. *Forests*, 12(6), Article 6. <https://doi.org/10.3390/f12060760>

Forests and forestry. (2023, November 17). [https://www.eea.europa.eu/en/topics/in-](https://www.eea.europa.eu/en/topics/in-depth/forests-and-forestry)

[depth/forests-and-forestry](https://www.eea.europa.eu/en/topics/in-depth/forests-and-forestry)

Gizachew, B., & Brunner, A. (2011). Density–growth relationships in thinned and unthinned

Norway spruce and Scots pine stands in Norway: *Scandinavian Journal of Forest*

Research. *Scandinavian Journal of Forest Research*, 26(6), 543–554.

<https://doi.org/10.1080/02827581.2011.611477>

Gxasheka, M., Gajana, C. S., & Dlamini, P. (2023). The role of topographic and soil factors on

woody plant encroachment in mountainous rangelands: A mini literature review.

Heliyon, 9(10), e20615. <https://doi.org/10.1016/j.heliyon.2023.e20615>

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W.,

Müller, A., Sumser, H., Hörren, T., Goulson, D., & Kroon, H. de. (2017). More than 75

percent decline over 27 years in total flying insect biomass in protected areas. *PLOS*

ONE, 12(10), e0185809. <https://doi.org/10.1371/journal.pone.0185809>

Hamilton, A. (2005). Species diversity or biodiversity? *Journal of Environmental*

Management, 75, 89–92.

Havašová, M., Ferenčík, J., & Jakuš, R. (2017). Interactions between windthrow, bark beetles

and forest management in the Tatra national parks. *Forest Ecology and Management*,

391, 349–361. <https://doi.org/10.1016/j.foreco.2017.01.009>

Hentschel, R., Rosner, S., Kayler, Z. E., Andreassen, K., Børja, I., Solberg, S., Tveito, O. E.,

Priesack, E., & Gessler, A. (2014). Norway spruce physiological and anatomical predisposition to dieback. *Forest Ecology and Management*, 322, 27–36.

<https://doi.org/10.1016/j.foreco.2014.03.007>

Huth, F., Wehnert, A., Tiebel, K., & Wagner, S. (2017). Direct seeding of silver fir (*Abies alba*

Mill.) to convert Norway spruce (*Picea Abies* L.) forests in Europe: A review. *Forest*

Ecology and Management, 403, 61–78. <https://doi.org/10.1016/j.foreco.2017.08.017>

Jaar 2023. (n.d.). Retrieved March 25, 2024, from

<https://www.meteohoogeveen.nl/joomla3/index.php/statistieken/2023/>

Jandl, R. (2020). Climate-induced challenges of Norway spruce in Northern Austria. *Trees,*

Forests and People, 1, 100008. <https://doi.org/10.1016/j.tfp.2020.100008>

Keesey, T. M. (2024). *PhyloPic*. PhyloPic.Org. <https://www.phylopic.org>

Klimo, E., & European Forest Institute (Eds.). (2000). *Spruce monocultures in Central Europe:*

Problems and prospects. European Forest Institute.

Kupferschmid, A. D., Brang, P., Schönenberger, W., & Bugmann, H. (2006). Predicting tree

regeneration in *Picea abies* snag stands. *European Journal of Forest Research*, 125(2),

163–179. <https://doi.org/10.1007/s10342-005-0080-8>

Kupferschmid, A., Schönenberger, W., & Wasem, U. (2002). Tree regeneration in a Norway

spruce snag after tree die-back caused by *Ips typographus*. *Forest Snow and*

Landscape Research, 77, 149–160.

Leidinger, J., Blaschke, M., Ehrhardt, M., Fischer, A., Gossner, M. M., Jung, K., Kienlein, S.,

Kózik, J., Michler, B., Mosandl, R., Seibold, S., Wehner, K., & Weisser, W. W. (2021).

Shifting tree species composition affects biodiversity of multiple taxa in Central

European forests. *Forest Ecology and Management*, 498, 119552.

<https://doi.org/10.1016/j.foreco.2021.119552>

Lyseng, M. P., Bork, E. W., Hewins, D. B., Alexander, M. J., Carlyle, C. N., Chang, S. X., &

Willms, W. D. (2018). Long-term grazing impacts on vegetation diversity, composition, and exotic species presence across an aridity gradient in northern temperate

grasslands. *Plant Ecology*, 219(6), 649–663. [https://doi.org/10.1007/s11258-018-](https://doi.org/10.1007/s11258-018-0824-4)

0824-4

Monk, C. D. (1983). Relationship of Life forms and Diversity in Old-Field Succession. *Bulletin*

of the Torrey Botanical Club, 110(4), 449–453. <https://doi.org/10.2307/2996278>

Obladen, N., Dechering, P., Skiadaresis, G., Tegel, W., Keßler, J., Höllerl, S., Kaps, S., Hertel, M.,

Dulamsuren, C., Seifert, T., Hirsch, M., & Seim, A. (2021). Tree mortality of European beech and Norway spruce induced by 2018-2019 hot droughts in central Germany.

Agricultural and Forest Meteorology, 307, 108482.

<https://doi.org/10.1016/j.agrformet.2021.108482>

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R.

B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M.,

Bolker, B., Borcard, D., Carvalho, G., Chirico, M., Caceres, M. D., Durand, S., ...

Weedon, J. (2022). *vegan: Community Ecology Package (2.6-4)* [Computer software].

<https://cran.r-project.org/web/packages/vegan/index.html>

Old Grol. (2024, April 13). *Old Grol*. Old Grol. <https://www.oldgrol.nl/>

Oulehle, F., & Hruška, J. (2005). Tree species (*Picea abies* and *Fagus sylvatica*) effects on soil

water acidification and aluminium chemistry at sites subjected to long-term

acidification in the Ore Mts., Czech Republic. *Journal of Inorganic Biochemistry*, 99(9),

1822–1829. <https://doi.org/10.1016/j.jinorgbio.2005.06.008>

Palm, K., Vodde, F., Tullus, T., Engelhart, J., & Jørgiste, K. (2022). Impact of different storm severity levels and post-storm management on understory vegetation richness, diversity and composition 19–20 years after wind disturbance. *Forest Ecology and Management*, 524, 120506. <https://doi.org/10.1016/j.foreco.2022.120506>

Pretzsch, H., Grams, T., Häberle, K. H., Pritsch, K., Bauerle, T., & Rötzer, T. (2020). Growth and mortality of Norway spruce and European beech in monospecific and mixed-species stands under natural episodic and experimentally extended drought. Results of the KROOF throughfall exclusion experiment. *Trees*, 34(4), 957–970. <https://doi.org/10.1007/s00468-020-01973-0>

Pretzsch, H., Schütze, G., & Biber, P. (2018). Drought can favour the growth of small in relation to tall trees in mature stands of Norway spruce and European beech. *Forest Ecosystems*, 5(1), 20. <https://doi.org/10.1186/s40663-018-0139-x>

R Core Team. (2021). *R: A language and environment for statistical computing*. <https://www.r-project.org/>

Ramirez, J. I., Jansen, P. A., den Ouden, J., Goudzwaard, L., & Poorter, L. (2019). Long-term effects of wild ungulates on the structure, composition and succession of temperate forests. *Forest Ecology and Management*, 432, 478–488. <https://doi.org/10.1016/j.foreco.2018.09.049>

Riffell, S., Verschuyf, J., Miller, D., & Wigley, T. B. (2011). Biofuel harvests, coarse woody debris, and biodiversity – A meta-analysis. *Forest Ecology and Management*, 261(4), 878–887. <https://doi.org/10.1016/j.foreco.2010.12.021>

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>

Schlyter, P., Stjernquist, I., Barring, L., Jönsson, A., & Nilsson, C. (2006). Assessment of the impacts of climate change and weather extremes on boreal forests in northern Europe, focusing on Norway spruce. *Climate Research*, 31, 75–84.

<https://doi.org/10.3354/cr031075>

Schneider, C. A., Rasband, W. S., & Eliceiri, K. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9(7), 671–675. <https://doi.org/10.1038/nmeth.2089>

Simler-Williamson, A. B., Rizzo, D. M., & Cobb, R. C. (2019). Interacting Effects of Global Change on Forest Pest and Pathogen Dynamics. In D. J. Futuyma (Ed.), *Annual Review of Ecology, Evolution, and Systematics*, Vol 50 (Vol. 50, pp. 381–403). Annual Reviews.

<https://doi.org/10.1146/annurev-ecolsys-110218-024934>

Smit, R., & Olff, H. (1998). Woody species colonisation in relation to habitat productivity.

Plant Ecology, 139(2), 203–209. <https://doi.org/10.1023/A:1009750216223>

Smith, C. Y., Moroni, M. T., & Warkentin, I. G. (2009). Snag dynamics in post-harvest landscapes of western Newfoundland balsam fir-dominated boreal forests. *Forest Ecology and Management*, 258(5), 832–839.

<https://doi.org/10.1016/j.foreco.2009.03.027>

Storaunet, K. O. (2004). Models to predict time since death of *Picea abies* Snags.

Scandinavian Journal of Forest Research, 19(3), 250–260.

<https://doi.org/10.1080/02827580410024142>

Storch, D., & Okie, J. G. (2019). The carrying capacity for species richness. *Global Ecology and Biogeography*, 28(10), 1519–1532. <https://doi.org/10.1111/geb.12987>

Biogeography, 28(10), 1519–1532. <https://doi.org/10.1111/geb.12987>

Tērauds, A., Brūmelis, G., & Nikodemus, O. (2011). Seventy-year changes in tree species

composition and tree ages in state-owned forests in Latvia: *Scandinavian Journal of*

Forest Research. *Scandinavian Journal of Forest Research*, 26(5), 446–456.

<https://doi.org/10.1080/02827581.2011.586647>

Thers, H., Bøcher, P. K., & Svenning, J.-C. (2019). Using lidar to assess the development of structural diversity in forests undergoing passive rewilding in temperate Northern Europe. *PeerJ*, 6, e6219. <https://doi.org/10.7717/peerj.6219>

Uroz, S., Oger, P., Tisserand, E., Cébron, A., Turpault, M.-P., Buée, M., De Boer, W., Leveau, J. H. J., & Frey-Klett, P. (2016). Specific impacts of beech and Norway spruce on the structure and diversity of the rhizosphere and soil microbial communities. *Scientific Reports*, 6(1), Article 1. <https://doi.org/10.1038/srep27756>

Weergegevens Hoogeveen 2023—Weerstatistieken KNMI. (n.d.). Retrieved March 25, 2024, from <https://weerstatistieken.nl/hoogeveen/2023>

Wermelinger, B. (2004). Ecology and management of the spruce bark beetle *Ips typographus*—A review of recent research. *Forest Ecology and Management*, 202(1), 67–82. <https://doi.org/10.1016/j.foreco.2004.07.018>

Xie, J., Fang, S., & Yan, Q. (2023). Effects of thinning on functional and phylogenetic diversity of regenerated woody plants in plantations over time. *Applied Vegetation Science*, 26(3), e12737. <https://doi.org/10.1111/avsc.12737>

Zaitsev, A. S., Chauvat, M., & Wolters, V. (2014). Spruce forest conversion to a mixed beech-coniferous stand modifies oribatid community structure. *Applied Soil Ecology*, 76, 60–67. <https://doi.org/10.1016/j.apsoil.2013.12.009>

Zeppenfeld, T., Svoboda, M., DeRose, R. J., Heurich, M., Müller, J., Čížková, P., Starý, M., Bače, R., & Donato, D. C. (2015). Response of mountain *Picea abies* forests to stand-replacing bark beetle outbreaks: Neighbourhood effects lead to self-replacement.

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Journal of Applied Ecology, 52(5), 1402–1411. <https://doi.org/10.1111/1365->

2664.12504

Supplementary figure 1

(S1): Species list

Species	Name latin	Name english	Name dutch	Type	Origin
Pabi	<i>Picea abies</i>	Norway spruce	Fijnspar	Coniferous	Exotic
Sauc	<i>Sorbus aucuparia</i>	Mountain ash	Wilde lijsterbes	Deciduous	Native
Rfra	<i>Rhamnus frangula</i>	Alder buckthorn	Sporkehout	Deciduous	Native
Pser	<i>Prunus serotina</i>	black cherry	Amerikaanse vogelkers	Deciduous	Exotic
Alae	<i>Amelanchier laevis</i>	Allegheny serviceberry	Drentse krentenboom	Deciduous	Exotic
Pmen	<i>Pseudotsuga menziesii</i>	Douglas fir	Douglaspars	Coniferous	Exotic
Lkae	<i>Larix kaempferi</i>	Japanese larch	Japanse lariks	Coniferous	Exotic
Fsylv	<i>Fagus sylvatica</i>	European beech	Beuk	Deciduous	Native
Iaqu	<i>Ilex aquifolium</i>	Common holly	Hulst	Deciduous	Native
Pnig	<i>Pinus nigra</i>	Black pine	Zwarte den	Coniferous	Exotic
Qrob	<i>Quercus robur</i>	English oak	Zomereik	Deciduous	Native
Sari	<i>Sorbus aria</i>	Whitebeam	Meelbes	Deciduous	Native
Psyl	<i>Pinus sylvestris</i>	Scots pine	Grove den	Coniferous	Exotic
Bspe	<i>Betula species</i>	Birch	Berk	Deciduous	Native